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Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna

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Summary

1 The cultivation and dissemination of alien ornamental plants increases their potential to invade. More specifically, species with bird-dispersed seeds can potentially infiltrate natural nucleation processes in savannas.

2 To test (i) whether invasion depends on facilitation by host trees, (ii) whether propagule pressure determines invasion probability, and (iii) whether alien host plants are better facilitators of alien fleshy-fruited species than indigenous species, we mapped the distribution of alien fleshy-fruited species planted inside a military base, and compared this with the distribution of alien and native fleshy-fruited species established in the surrounding natural vegetation.

3 Abundance and diversity of fleshy-fruited plant species was much greater beneath tree canopies than in open grassland and, although some native fleshy-fruited plants were found both beneath host trees and in the open, alien fleshy-fruited plants were found only beneath trees.

4 Abundance of fleshy-fruited alien species in the natural savanna was positively correlated with the number of individuals of those species planted in the grounds of the military base, while the species richness of alien fleshy-fruited taxa decreased with distance from the military base, supporting the notion that propagule pressure is a fundamental driver of invasions.

5 There were more fleshy-fruited species beneath native *Acacia tortilis* than beneath alien *Prosopis* sp. trees of the equivalent size. Although there were significant differences in native plant assemblages beneath these hosts, the proportion of alien to native fleshy-fruited species did not differ with host.

6 Synthesis. Birds facilitate invasion of a semi-arid African savanna by alien fleshy-fruited plants, and this process does not require disturbance. Instead, propagule pressure and a few simple biological observations define the probability that a plant will invade, with alien species planted in gardens being a major source of propagules. Some invading species have the potential to transform this savanna by overtopping native trees, leading to ecosystem-level impacts. Likewise, the invasion of the open savanna by alien host trees (such as *Prosopis* sp.) may change the diversity, abundance and species composition of the fleshy-fruited understorey. These results illustrate the complex interplay between propagule pressure, facilitation, and a range of other factors in biological invasions.

Key-words: biological invasions, clumping, frugivorous birds, impacts, invasive species, mutualisms, ornithochory, propagule pressure, seed dispersal, South Africa, spatial analysis, vegetation change

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Introduction

Dispersal of seeds by birds is essential for the maintenance of tree and shrub populations and for structuring vegetation in many ecosystems (Kollmann 2000). By perching and nesting in trees, frugivorous birds direct seeds of fleshy-fruited plants to subcanopy sites (Snow 1976). Such dispersal may lead to changes in vegetation that, depending on the management perspective and the plant species involved, may be viewed as succession (Cowling *et al*. 1997), recolonization after anthropogenic disturbances (Milton *et al*. 1997; Holl 2002), or invasion (Gimeno & Vila 2002; Buckley *et al*. 2006).

Birds are particularly important for determining the clumped distribution of fleshy-fruited plant species (Bews 1917; Archer *et al*. 1988). Where tree cover is incomplete, establishment of fleshy-fruited plants occurs predominantly under tree canopies, and far less in the open, because frugivorous birds perch in tree canopies (Debussché & Isenmann 1994; Vierera *et al*. 1994; Pausas *et al*. 2006) and subcanopy microsite conditions are favourable for seed germination and seedling establishment (Belsky *et al*. 1993; Verdú & García-Fayos 1996). The process of shrub-clump formation resulting from the distribution of seed of a number of fleshy-fruited species to a single perch site is known as 'nucleation' (viz. Pausas *et al*. 2006), because such clumps tend to grow around a single founder plant (or nucleus).

In savanna systems worldwide, isolated trees represent focal points for bird activity (Dean *et al*. 1999), for recruitment of bird-dispersed plants (Smith & Goodman 1987; Flores-Flores & Yeaton 2000), and for the development of species-rich clumps of fleshy-fruited plants (Archer *et al*. 1988; Skarpe 1991). Typically, the interactions between herbivory, avian seed dispersal and fire lead to the cycle, shown in Fig. 1, whereby a

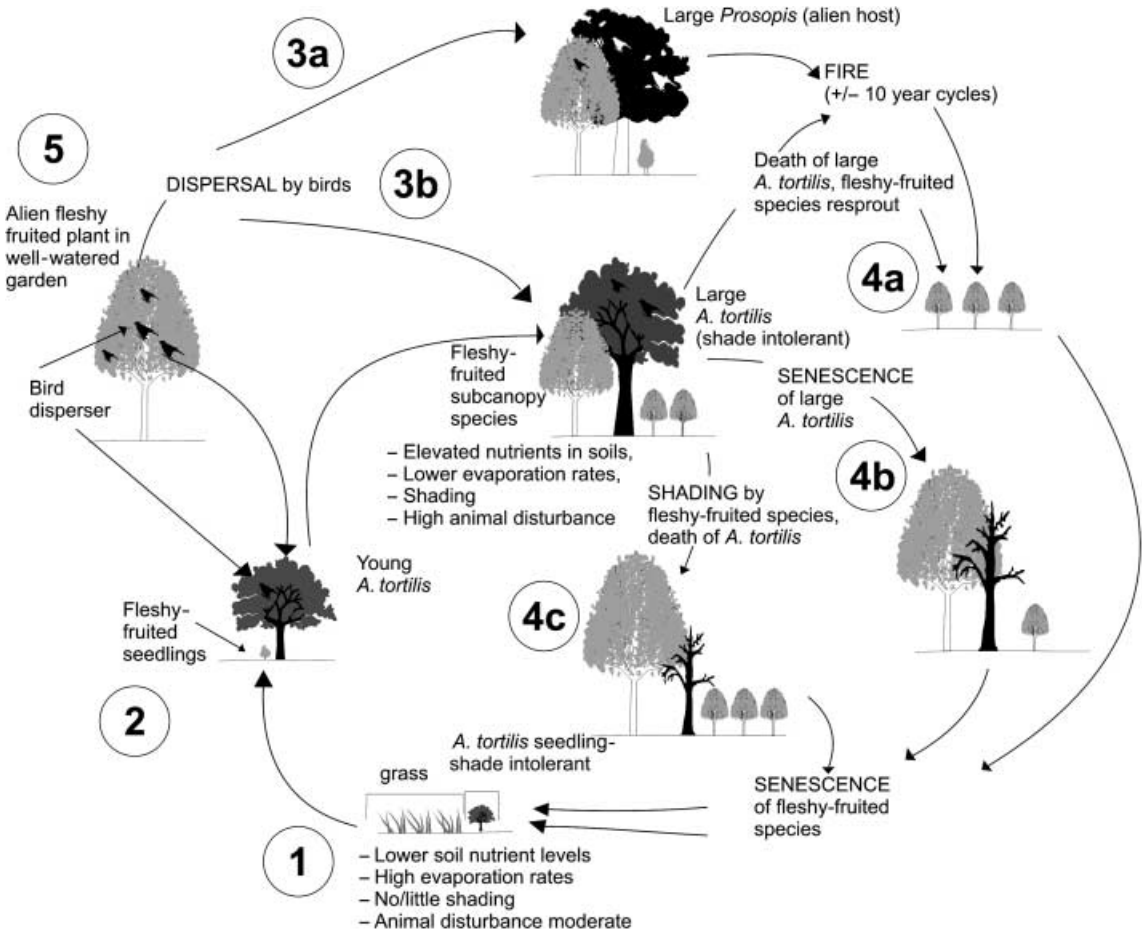

Fig. 1 Conceptual model of the nucleation process in open semi-arid savanna (adapted from Dean *et al.* 1999). Invasive alien species have the potential to co-opt natural processes in several ways. (1) New host seedlings of both native (*Acacia* spp.) and alien (*Prosopis* sp.) species germinate in the open. (2) As the seedlings grow, birds begin to use them as perch sites, thereby dispersing fleshy fruit to host trees. (3) A subcanopy assemblage of fleshy-fruited shrubs and trees develops under large host trees, the composition of which differs between native and alien host species. (4) The host tree can be killed in a number of ways: (a) Fire often kills large host trees; crucially, the subcanopy plant assemblage (which can differ both due to the presence of alien seedlings, and between native and alien hosts) can determine fire intensity and duration by altering fuel quality and distribution; (b) fleshy-fruited indigenous *Rhus lancea* and alien *Celtis* sp. and *Schinus molle* shade out host trees; (c) host trees, and eventually fleshy-fruited trees, senesce and are replaced by open habitat suitable for new host trees. (5) Seeds of alien fleshy-fruited trees in gardens are dispersed into subcanopy sites in natural savanna by birds, and may change the dynamics of the savanna. In particular, by competing with certain native fleshy-fruited species for disperser attention, alien species may reduce dispersal rates for native species.

wind- or mammal-dispersed tree establishes in the grassland, attracting birds, many of which feed on both insects and fruits. The birds transport seeds of a variety of fleshy-fruited plants to a perch site in the tree. Shade-adapted seedlings establish below the canopy, forming a bush clump that attracts frugivorous birds that bring more seeds. Over time, fleshy-fruited species may grow to overtop the original host tree, outcompeting it for light (Yeaton & Manzanares 1986; Flores-Flores & Yeaton 2000). Eventually senescence, with or without fire, returns the clump to grassland.

In theory, the addition of new (i.e. alien) bird-dispersed plant species could alter the processes shown in Fig. 1 in many ways. The timing and abundance of propagule availability could clearly mediate the type and magnitude of influence of the added species. For example, artificially elevated propagule pressure (due to the widespread planting, feeding and watering of ornamentals and copious seed production in the absence of natural enemies) could enhance the ability of alien species to both establish and to then influence prevailing processes (Lockwood *et al*. 2005). In a meta-analysis of characteristics of invasiveness, Colautti *et al*. (2006) found propagule pressure was consistently associated with invasion success. Both for this reason, and because propagule pressure models invasions as a probabilistic process, Colautti *et al*. (2006) suggested that it should form the basis of a null model for biological invasions.

In this paper the terms 'alien', 'native' and 'invasive' follow definitions proposed by Pyšek *et al*. (2004). Native plants are 'taxa that have originated in a given area without human involvement or that have arrived there without intentional or unintentional intervention of humans from an area in which they are native', whereas alien taxa are those 'whose presence [in a given area] is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien'. Invasive plants are a subset of naturalized plants that produce and disperse many reproductive offspring, and thus have the potential to spread over a large area.

The relationship between birds and fleshy-fruited plants is so widespread and general that new mutualisms (Richardson *et al*. 2000a) rapidly develop between birds (native and alien) and alien fleshy-fruited species, enabling the birds to disperse the plant propagules over long distances from established gardens to suitable microsites in natural vegetation. The addition of new (alien) tree species to an ecosystem provides further, perhaps alternative, foci for the deposition and establishment of fleshy-fruited alien species. Such mutualisms are clearly crucial facilitators of invasions. Simberloff & Von Holle (1999) suggest that synergistic interactions among invaders that accelerate invasions and/or amplify their effects on native communities can be seen as 'invasional meltdown'. The important effects that invasions may have on naturally occurring mutualisms are less widely appreciated, but have momentous implications for biodiversity in invaded ecosystems (Traveset & Richardson 2006).

Arid ecosystems in most regions have been less affected by biological invasions than more mesic ecosystems (Loope *et al*. 1988; Milton *et al*. 1999). This may be because the subset of drought-hardy plants is smaller. Other contributing reasons may be that establishment opportunities (for example the occurrence of substantial postgermination rains) are more rare (and therefore slower to become evident) and/or that fewer species and individuals of alien species have been introduced to arid, as opposed to more mesic, regions. The phenomenon of alien plant invasions may therefore be an emerging problem in arid parts of South Africa. Established invasive plants have spread more quickly in arid than in wetter areas of South Africa (Wilson *et al*. 2007). Certainly, plant invasions have been much less studied in arid parts of South Africa, and information on the processes of invasion in such areas is urgently needed (Richardson & van Wilgen 2004).

The low density of trees, and therefore subcanopy microsites, in semi-arid savannas results in strongly clumped dispersal of seed by birds (Dean *et al*. 1999). This clumping increases the probability that even small individuals of alien plant species present at low density could be detected.

We therefore undertook this study of the early stages of a plant invasion to test the following hypotheses:
1. invasion by alien fleshy-fruited trees and shrubs into semi-arid savanna is aided by the presence of host trees;
2. propagule pressure determines invasion probability; and
3. alien host plants are better facilitators than native host species of invasion by alien fleshy-fruited species, i.e. the conditions exist for invasional meltdown.

Materials and methods

STUDY SITE

The study was conducted in and around the Diskobolos Military Base (Aleksanders Fontein), 2 km south of Kimberley in South Africa's Northern Cape province (28°47′ S, 24°47′ E, 1198 m a.s.l., Fig. 2). The climate is semi-arid and the mean annual rainfall is 414 mm, most of it from thunder storms in late summer. Mean daily temperatures range from 33 °C to 18 °C in January, and from 19 °C to 3 °C in July (South African Weather Bureau 2003). The military base was established in 1967, and many trees of several species, all now well established, were planted along the streets to provide shade and decoration at this time. The military and associated personnel also maintain gardens in which many more plants are cultivated, most of them alien or extra-limital species (i.e. species indigenous to South Africa but outside their natural distribution ranges).

The savanna vegetation surrounding the military base is classified as Kimberley Thorn Bushveld (Low & Rebelo 1996). The dominant native tree species is

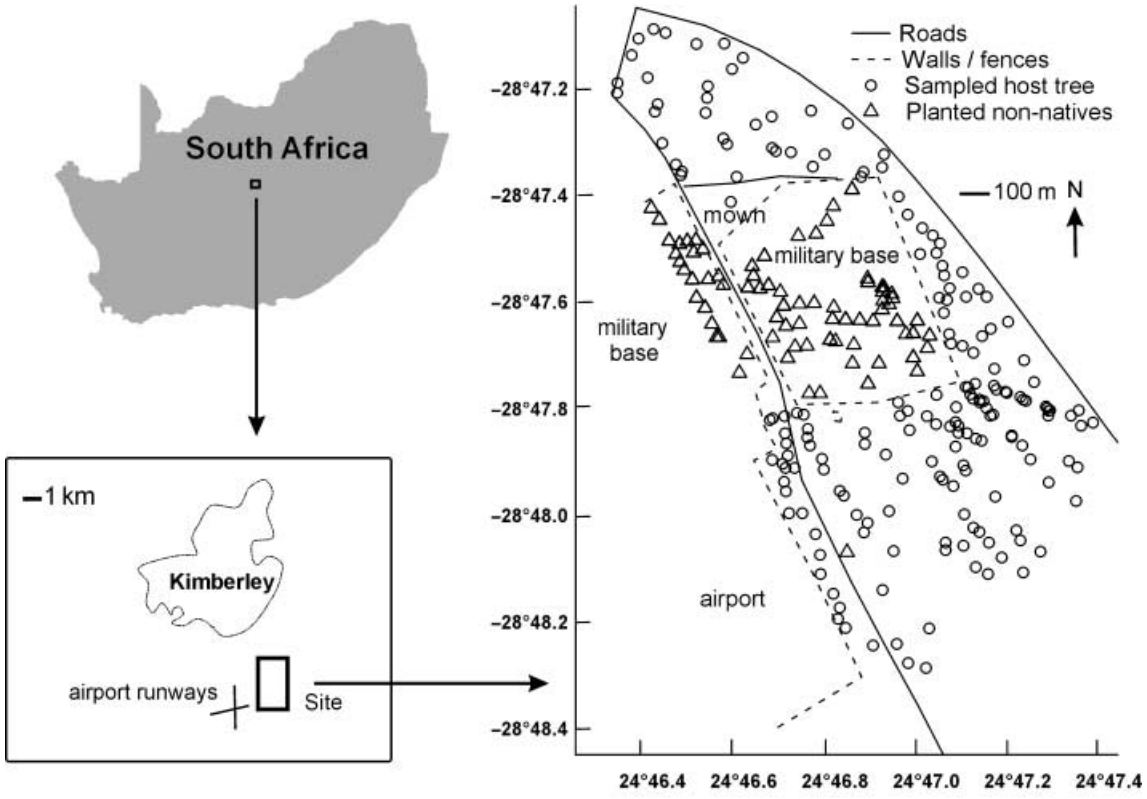

Fig. 2 Map of the study site showing its position in South Africa and in relation to the town of Kimberley. The military base and associated alien plants were in the centre of the study site. The triangles refer to any planted alien fleshy-fruited species. Additional sources of alien plant propagules (e.g. suburbs and farm buildings) were more than 3 km from the study site.

Acacia tortilis (Fabaceae: Mimosoideae). Associated with this are native bird-dispersed plants including *Rhus lancea* (Anacardiaceae) that have potential to overtop *A. tortilis*, and various subcanopy shrubs, lianas and herbs. Tree cover varies between 5% and 15% at the hectare scale (based on estimates made from aerial photographs). The planting of alien trees in adjacent areas (e.g. at the nearby Kimberley Airport) is minimal, thus making the military base and surrounding savanna ideal for a study of plant invasion from a single source. There are also three long-established invasive plant species absent from the base but already present at the landscape scale in the surrounding vegetation. These are pod-bearing *Prosopis* sp. (Fabaceae: Mimosoideae; mesquite) (hybrids of *P. glandulosa* and several other alien *Prosopis* taxa), and the fleshy-fruited species *Opuntia ficus-indica* (Cactaceae) and *Atriplex semibaccata* (Chenopodiaceae).

Nomenclature for indigenous plant species follows Germishuizen & Meyer (2003), and for alien plant species, Henderson (2001). Bird nomenclature follows Hockey *et al*. (2005).

SAMPLING DESIGN AND DATA COLLECTION

Inside the military base, all adult fleshy-fruited plants of species not occurring naturally in the Kimberley area, and that would represent potential propagule sources for invasion in the surrounding savanna, were identified and mapped. Outside the base, 181 sites, each comprising a canopy tree and an adjacent plot in herbaceous vegetation, were surveyed. The information recorded included (i) tree species, (ii) height (estimated to the nearest metre), (iii) minimum and maximum canopy radius, (iv) geographical coordinates, (v) soil type (classified as sand, loam or calcrete (also known as caliche)), and (vi) presence or absence of any obvious anthropogenic or natural disturbance, such as mining, construction, paths, or burrows of porcupines (*Hystrix africaeaustralis*) and aardvarks (*Orycteropus afer*). The fleshy-fruited plant species (all life-forms) occurring under each tree were recorded in seven height classes (0–0.05 m, 0.05–0.1 m, 0.1–0.2 m, 0.2–0.40 m, 0.40 m–canopy, in canopy, emergent). The open plot (5×5 m) was placed 20 m from the canopy of each sampled tree in the direction least affected by neighbouring trees, and was surveyed in the same way for fleshy-fruited plant species. The spatial positioning of the surveyed plants is given in Fig. 2. All surveys were undertaken during April 2006, following autumn rain, when the probability of finding young seedlings was greatest.

DATA ANALYSES

We considered three main questions related to the processes and hypotheses outlined. First, to what extent is the distribution of seedlings of a species defined by where adult plants are (processes 2 and 5 on Fig. 1;

hypothesis 1)? Secondly, what were the main determinants of seedling species richness and abundance, in particular how did the relative proportion of aliens to natives vary with distance from the source of most of the aliens (the military base) (processes 2 and 5 on Fig. 1; hypothesis 2)? Thirdly, does the identity of the host tree affect the assemblage composition of the fleshy-fruited plants species (process 3a, 3b and 4c on Fig. 1; hypothesis 3)?

To examine the effect of distance on the probability of any particular species dispersing to a site, we modelled species abundance under a host tree as explained by the presence of disturbance, the log of the Euclidean distance to the closest mature plant, and the log of canopy extent using a generalized linear model with negative binomial errors. As a measure of canopy extent we used the product of the canopy radius and canopy height as this was the best explanatory variable for patterns of species richness (see results), and other measures of canopy extent, e.g. canopy volume, gave qualitatively similar results. The minimum adequate model was arrived at by step-wise deletion from the maximal model. As the species abundance data were often highly skewed (a few sites having many seedlings), generalized linear models with negative binomial errors were used (glm.nb in Venables & Ripley 2002). Subcanopy individuals that were the same species as the host tree were excluded, as were species adapted for dispersal by wind. Therefore the analyses only explore individuals that were dispersed by birds or other animals. For native trees, the distance to the centre of the military base was measured to test whether proximity affected their frequency.

Patterns in species richness were investigated by fitting a generalized linear model with Poisson errors. The minimal adequate model was arrived at by step-wise deletion from the maximal model (with a cut-off of $P(\times) = 0.05$). The percentage deviance explained by each significant factor was determined by the change in explained deviance when the factor was dropped from the minimum adequate model (Lobo *et al*. 2002). To explore the spatial structure of the variation, a minimum adequate trend surface model was produced (Legendre & Legendre 1998). All significant environmental and spatial terms were then added in a full model, and the spatially structured components of the environmental variables were assessed by comparing the percentage deviance explained by the factor in a model without the trend surface terms with the deviance explained by the factor in a spatially implicit trend surface model. In most cases the residuals were not over-dispersed, but, as a check of the robustness of the results, the models were re-run using a quasi-Poisson error structure.

The process was repeated for alien species richness and native species richness separately. To test for differences between germination and establishment, we re-ran all analyses excluding records of plants < 0.1 m tall, which we assumed to represent seedlings. Finally, to explicitly test for differences between the relative species richness of natives and aliens found under the hosts, we used generalized linear models with binomial errors.

To ascertain whether fleshy-fruited plant assemblages were different when they occurred beneath native (i.e. *A. tortilis*) or alien (i.e. *Prosopis*) host trees, we constructed similarity matrices of log abundance data using a Bray-Curtis similarity measure, and then used an analysis of similarities (ANOSIM) to detect significant differences. These comparisons were carried out on data sets from which seedlings had been excluded (i.e. subcanopy plants < 0.1 m in height), as we were interested in the final species composition beneath trees and not species that germinate but do not establish. Those trees for which removal of seedlings left no subcanopy fleshy-fruited plants could not be analysed and were excluded. We also analysed similarities in subcanopy alien species composition, using the same methods as above, to ascertain whether alien species assemblages were significantly different as a function of native and alien host tree, canopy extent and distance from base. These analyses were done using PRIMER vs. 5 (Clarke & Gorley 2001, 2006).

Results

IMPORTANCE OF HOST TREES AS ESTABLISHMENT SITES

The presence of host trees appeared to be essential for invasion by alien fleshy-fruited trees and shrubs (hypothesis 1). While 19 native and 12 alien fleshy-fruited species were found growing beneath the tree canopies, 11 native (but no alien) fleshy-fruited species were recorded in the plots outside the tree canopies (Tables 1 and 2; the ratio of alien to native species was higher under the canopy than in the open, Fisher's test $P = 0.018$; *Thesium hystrix* and one *Asparagus* species were found in the outside plots but not under the canopy, so the total recorded species richness was 33). Of the plots outside the canopy, 62 contained no fleshy-fruited species, 97 had one species, 21 had two species and one had three species; of those species found outside the canopy only *Lycium cinereum*, *Lycium hirsutum* and *Pollichia campestris* were present in more than three plots. In contrast, under the canopy half the species were present under more than 10 host trees, and median species richness per host tree was five (range 0–14). There was no significant correlation between species richness under tree canopies and in the adjacent grassy plots (Spearman's rank correlation, $P = 0.20$).

There were positive relationships between site occupancy and seedling abundance for both small (< 0.1 m in height) and larger individuals (Fig. 3a,b, $P < 0.01$). While these relationships did not differ significantly between natives and aliens, the most abundant native fleshy-fruited tree species (*Rhus lancea*) dominated assemblages of seedlings < 0.1 m in height, and consequently had a large influence on the analysis (Cook's distance > 1, Fig. 3a). If small *Rhus lancea* seedlings

Table 1 Alien or extra-limital fleshy-fruited species found in the study area. Species are ranked according to a qualitative assessment of invasion probability. Species that have mature individuals in the field and are frequent in natural vegetation are most likely to become invasive. Those species not found outside the base were ranked according to decreasing propagule pressure (more individuals of a species should provide a stronger test of its invasion potential). The distance relationship is a test of whether distance from the nearest mature plant (or the centre of the base if no mature plants were recorded) significantly affects the abundance of the species at a site (i.e. whether there is evidence of dispersal limitation). The combined list of *P*-values for native (Table 2) and aliens (this table) was corrected for multiple comparisons using the false detection rate method (*P*-adjust function in R). Columns marked NA denote where tests could not be performed (e.g. the species was not found outside the base, or only one or two individuals were recorded)

List of species ordered by invasion probability	Life-form	No. of mature plants inside base	No. of trees under which the species was found	Distance relationship§	Percentage seedlings (< 0.1 m)	Individuals in adult size class?
Species found inside the base						
Celtis sp.†	Tree	18	60	–	35	Yes
Schinus molle†‡	Tree	32	50	**	59	Yes
Rhus pendulina	Tree	70	22	***	13	Yes
Melia azedarach†‡	Tree	153	11	(*)	63	Yes
Olea europaea ssp. *africana*	Tree	6	11	***	17	Yes
Punica granatum	Tree	27	7	***	0	Yes
Morus alba†	Tree	16	6	–	85	perhaps
Cotoneaster sp.†	Shrub	11	3	–	0	Yes
Brachychiton populneus†	Tree	34	14	–	78	No
Arecaceae sp. 1	Tree	3 (/ only)	0	NA	NA	NA
Arecaceae sp. 2	Tree	1 (/ only)	0	NA	NA	NA
Coprosma sp.	Shrub	1	0	NA	NA	NA
Crategus sp.†	Tree	1	0	NA	NA	NA
Cydonia oblonga	Tree	1	0	NA	NA	NA
Ferocactus sp.	Succulent	1	0	NA	NA	NA
Kiggelaria africana	Tree	1	0	NA	NA	NA
Phoenix reclinata	Tree	1	0	NA	NA	NA
Prunus cerasifera†	Tree	1	0	NA	NA	NA
Ficus carica	Tree	2	0	NA	NA	NA
Malus domestica	Tree	2	0	NA	NA	NA
Rosa sp.†	Shrub	2	0	NA	NA	NA
Rubiaceae sp.	Shrub	2	0	NA	NA	NA
Dovyalis caffra	Shrub	3	0	NA	NA	NA
Eriobotrya japonica†		4	0	NA	NA	NA
Phoenix dactylifera	Tree	4	0	NA	NA	NA
Vitex sp.	Shrub	4	0	NA	NA	NA
Vitis vinifera	Vine	4	0	NA	NA	NA
Koelreuteria paniculata		5	0	NA	NA	NA
Jasminum sp.	Vine	6	0	NA	NA	NA
Rosaceae species	Shrub	6	0	NA	NA	NA
Duranta erecta	Tree	7	0	NA	NA	NA
Prunus armeniaca	Tree	7	0	NA	NA	NA
Prunus persica	Tree	9	0	NA	NA	NA
Pyracantha sp.†	Shrub	11	0	NA	NA	NA
Maclura pomifera		13	0	NA	NA	NA
Ligustrum lucidum†	Tree	20	0	NA	NA	NA
Poncirus sp.		20	0	NA	NA	NA
Citrus sp.	Tree	32	0	NA	NA	NA
Rosa damascena	Shrub	76	0	NA	NA	NA
Species not found inside the base						
Atriplex semibaccata	Herb	0	7	–	71	Yes
Echinopsis spachiana†	Succulent	0	1	NA	0	Yes
Opuntia ficus-indica†	Succulent	0	8	–	0	Yes

†A declared invasive weed or a weed proposed as a potential invasive (from Henderson 2001).
‡Found as host trees.
–, $P > 0.1$; (*), $0.1 > P \geq 0.05$; *, $0.05 > P \geq 0.01$; **, $0.01 > P \geq 0.001$; ***, $P < 0.001$.

were excluded from the analysis, site occupancy, relative to seedling abundance, was significantly lower for alien than native species, indicating a higher degree of clumping in deposition of seed of aliens, potentially linked to the propagules arising primarily in the military base.

PROPAGULE PRESSURE AND INVASION PROBABILITY

The survey inside the military base revealed that 39 fleshy-fruited plant species (573 individuals) that do not occur naturally in the Kimberley area were in

Table 2 Fleshy-fruited species native to the region that were found in the study. See Table 1 for more details

List of species	Life-form	No. of trees under which the species was found	No. of grassland plots in which the species was found	Distance relationship (under canopy)	Distance relationship (outside canopy)	Percentage of all individuals that are small seedlings (< 0.1 m)
Asparagus cooperi†	Shrub	59	2	***	NA	13
Asparagus nelsii	Shrub	0	1	NA	NA	NA
Cucumis africanus	Vine	7	2	–	NA	50
Diospyros lycioides	Tree	119	3	–	NA	31
Ehretia alba†	Shrub	27	NA	*	NA	3
Grewia flava	Shrub	13	NA	–	NA	20
Kedrostis nana	Vine	1	NA	NA	NA	0
Lantana rugosa	Shrub	2	NA	NA	NA	0
Lycium cinereum	Shrub	100	106	–	–	7
Lycium hirsutum	Shrub	60	7	–	–	6
Pollichia campestris	Herb	101	16	–	–	9
Rhus burchellii	Shrub	2	NA	NA	NA	0
Rhus lancea‡	Tree	130	1	–	NA	97
Rhus tomentosa	Tree	1	NA	NA	NA	0
Solanum incanum	Herb	1	NA	NA	NA	0
Solanum sp.	Herb	1	NA	NA	NA	100
Solanum supinum	Herb	3	NA	–	NA	50
Solanum tomentosum	Herb	14	1	–	NA	0
Thesium lineare	Shrub	1	NA	NA	NA	0
Thesium hystrix	Shrub	0	1	NA	NA	NA
Ziziphus mucronata‡	Tree	117	1	–	NA	29

†More individuals found away from the base.
‡Found as host trees.

cultivation, most as ornamentals and shade trees (e.g. *Melia azedarach*, *Schinus molle*, *Rhus pendulina*) or for fruit (e.g. *Punica granatum*, *Prunus persica*, *Prunus armeniaca*). Only nine of these species were recorded in the surrounding savanna. Of these, two (*Olea europaea* ssp. *africana* and *Rhus pendulina*) are native to South Africa but not to the local area. The number of seedlings outside the base was strongly correlated with the number of mature plants found inside the base (Fig. 4, $P < 0.01$), and no species that had fewer than five individuals inside the base was found outside it. Seed size of alien species explained neither distance dispersed nor number of individuals found outside the base. These observations are in agreement with hypothesis 2, namely that propagule pressure determines invasion probability.

We also used size-class histograms (see Fig. S1 in Supplementary Material for examples) to assess the probability of invasion for the alien species encountered (Table 1). Size-class distributions differed considerably among species. Whereas all the native species were represented as mature individuals, two of the alien tree species were present only as seedlings or saplings.

When investigating how far the alien species had dispersed from the military base, we included disturbance and canopy extent as covariates because trees sampled

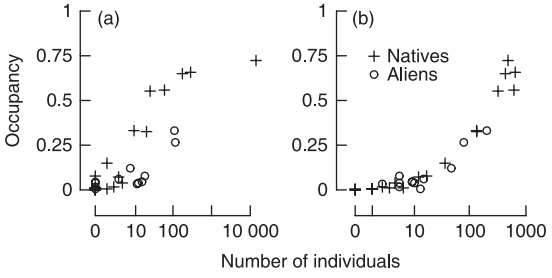

Fig. 3 Occupancy (proportion of the total number of trees that a species is found under) plotted against number of individuals found of that species for (a) native or alien individuals < 0.1 m in height and (b) native or alien individuals > 0.1 in height. Occupancy is calculated from the data for all size categories. Observations of a species growing beneath an intra-specific host were discounted in both the calculation of number of sub-canopy individuals and occupancy.

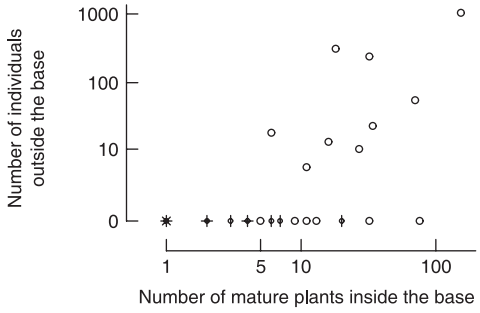

Fig. 4 The abundance of alien species outside the base is strongly dependent on the number of trees planted in the base (i.e. propagule pressure). Multiple points are plotted as 'sunflowers' with the number of leaves ('petals') representing the number of points.

further away tended to have larger canopies ($P < 0.05$) and more of the sites closer to the base were disturbed ($P < 0.001$). There was, however, no significant correlation between distance to the military base and host plant identity ($P = 0.35$) or soil type ($P = 0.51$ for sand, $P = 0.55$ for calcrete), so these factors were not included here. Three types of distribution patterns for fleshy-fruited species were identified (Fig. S2, Table 1): density higher closer to the military base or adult plants; density higher further from the military base; and density independent of distance from the base (most native species and some alien species). The alien species *Olea europaea* ssp. *africana*, *Rhus pendulina* and *Punica granatum* were strongly restricted to sites closer to mature conspecifics. *Schinus molle* and *Melia azedarach* seedlings also tended to occur close to adult trees (Table 1), but several mature individuals occurred outside the military base and so it would be problematic to infer the species was only dispersing to areas close to the base. Of the natives, only an *Asparagus* species and *Ehretia rigida* were affected by proximity to the base, and, in these cases, they were more abundant further from the base (Table 2). There were no significant trends for the other species.

HOST EFFECT (I.E. NATIVE OR ALIEN) ON SPECIES RICHNESS PATTERNS

The host species in the study represented similar geometric shapes in terms of canopy height and radius ($F_{10,175} = 0.975$, $P = 0.47$). Similarly, the relationship between height and radius was not significantly different between the *Prosopis* and *Acacia tortilis* trees sampled ($F_{2,155} = 3.01$, $P = 0.052$). Therefore, any differences in host suitability should be ascribed to properties of the host (e.g. differences in canopy structures or shade) and not larger areas *per se*.

Subcanopy fleshy-fruited species richness declined with distance from the military base for *Prosopis* sp. but was independent of distance for *Acacia tortilis* (Fig. 5, Table 3a). The parameter estimates are such that across all observed distances from the base the subcanopy species richness of *Prosopis* is predicted to be less than that for *Acacia tortilis*. Total subcanopy fleshy-fruited species richness under *Prosopis* sp. and *Acacia tortilis* increased with canopy extent (Fig. 6), and was lower in more disturbed sites (Table 3a).

Overall these four factors (distance, canopy extent, host identity and disturbance) explained 41.6% of the model deviance, and the data were well described by a Poisson distribution (deviance per degree of freedom of 1.04). Canopy extent explained more variation than canopy radius (total model deviance explained of 37.8%), canopy height (39.0%), or canopy volume (40.5%), and if the various measures of the canopy dimensions were included in the maximal model only canopy extent remained in the minimum adequate model. When a trend surface model was considered, disturbance was no longer a significant factor, but the percentage variance explained by the other factors did not change much. Soil type (loam, sand and loam, or calcrete and loam) did not have any significant effects.

When only natives were considered, the only significant effects were host, canopy extent and disturbance (Table 3b). Moreover, disturbance was not significant in the trend surface model, so the native species richness is in fact mostly described here by the size and species identity of the host tree. This qualitative result was the same if all host trees were included.

Species richness of aliens was explained by canopy extent, soil type and an interaction between host and distance from the military base (Table 3c). There were no significant differences in the proportions of species that were alien under *Prosopis* sp. and *Acacia tortilis* ($P(\times) = 0.077$), and similarly there was no effect of host plant if all hosts were considered ($P(\times) = 0.174$). This is contrary to the prediction that non-native host plants would facilitate invasions (hypothesis 3). However, the

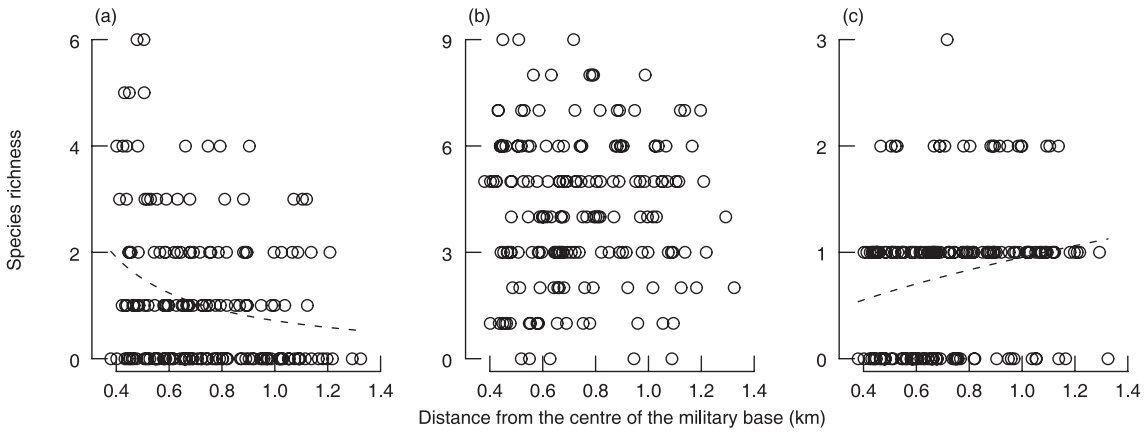

Fig. 5 Species richness of fleshy-fruited plant species against distance from the centre of the military base for (a) alien species, (b) native species found under tree canopies, and (c) native species found in grassland adjacent to the plots. The dotted lines are significant relationships from a generalised linear model with Poisson errors of species richness ~ log[distance]. Note, the relationship for aliens is also affected by host tree identity (see Table 3).

Table 3 (a) Minimal adequate model to explain total species richness under the canopy (log-link function). The estimates and standard errors shown are for each factor level, the *P*-value and percentage deviance are for the factor as a whole. Total percentage of deviance explained can sum to greater than the explained percentage deviance because of colinearity between the factors (e.g. trees further away from the military base tended to be slightly smaller and so in the absence of distance from the base, the parameter for canopy extent in the model will explain a portion of the variance attributable to distance). Results were qualitatively similar if all host plants were included in the analyses. Distance from the base and the volume of the subcanopy were both log-transformed. Null deviance (for model without spatial component): 255.30 on 149 degrees of freedom. Residual deviance: 149.46 on 144 degrees of freedom. (b) Minimal adequate model to explain native species richness under the canopy (log-link function). Null deviance (for model without spatial component): 163.25 on 149 degrees of freedom. Residual deviance: 107.84 on 146 degrees of freedom. (c) Minimal adequate model to explain alien species richness under the canopy (log-link function). Null deviance (for model without spatial component): 271.48 on 149 degrees of freedom. Residual deviance: 172.21 on 143 degrees of freedom. (d) Minimal adequate model to explain the relative proportion of native to alien species richness under the canopy (logit-link function). Null deviance (for model without spatial component): 189.26 on 153 degrees of freedom. Residual deviance: 145.87 on 149 degrees of freedom

	Model without spatial component				Trend surface model	
Model parameters	Estimate	SE	*P*-value	Deviance (%)	*P*-value	Deviance (%)
(a) Total species richness*						
Intercept	–0.0316	1.04	–	–	–	–
Host (*Prosopis* sp.)	4.02	2.04	–	14.0	–	12.9
Canopy extent	0.459	0.0546	< 0.001	27.6	< 0.001	30.5
Disturbance	–0.185	0.0802	0.020	2.1	0.13	0.9
Distance	0.0306	0.295	–	0.2	–	0.4
Host: distance	–1.62	0.722	0.025	2.0	0.019	2.2
Overall				41.6		50.7
(b) Native species richness*						
Intercept	0.695	0.164				
Host (*Prosopis* sp.)	–0.524	0.112	< 0.001	15.0	< 0.001	12.5
Canopy extent	0.351	0.0599	< 0.001	20.8	< 0.001	26.6
Disturbance	–0.241	0.0879	0.005	4.7	0.125	1.4
Overall				33.9		44.4
(c) Alien species richness†						
Intercept	1.55	1.98	–	–	–	–
Host (*Prosopis* sp.)	11.3	5.24	–	5.1	–	5.0
Canopy extent	0.96	0.128	< 0.001	22.3	< 0.001	18.2
Soil (sand)	2.33	0.753	0.008	3.6	0.118	1.6
Soil (calcrete)	–1.06	0.593	–	–	–	–
Distance	–1.42	0.662	–	4.1	–	0.5
Host : distance	–4.34	1.90	0.016	2.1	0.0053	2.9
Overall				36.6		45.0
(d) Proportion of native to alien species†						
Intercept	3.90	2.0789	–	–	–	–
Canopy extent	0.5837	0.1403	< 0.001	9.4	0.005	4.2
Soil (sand)	2.4640	0.9557	0.021	4.1	0.24	1.5
Soil (calcrete)	–0.9960	0.6526	–	–	–	–
Distance Overall	–2.4533	0.6954	< 0.001	6.8	0.28	0.6

*Base model is host = *Acacia tortilis*, no disturbance
†Base model is host = *Acacia tortilis*, soil = loam

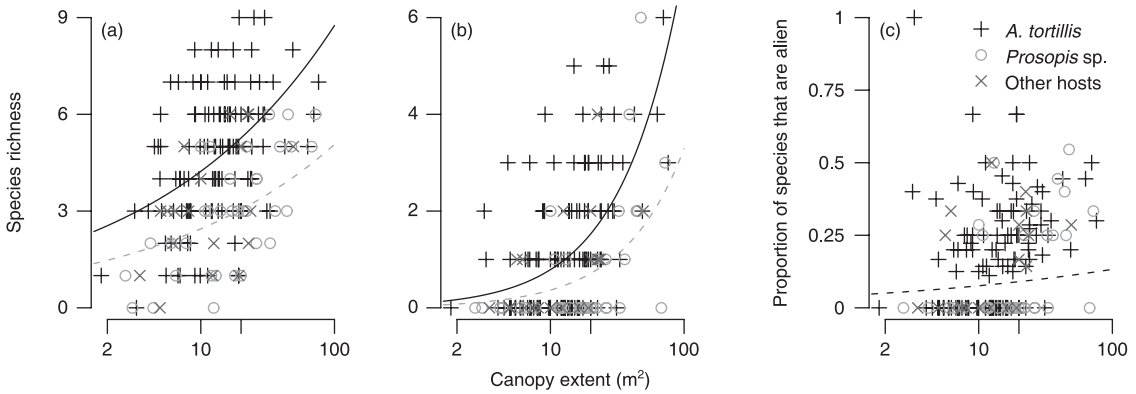

Fig. 6 The effect of canopy extent on the fleshy-fruited sub-canopy species: (a) native species richness, (b) alien species richness, and (c) the proportion of species that are alien. Alien species richness increases faster with canopy extent than does native species richness. The fitted lines in (a) and (b) are significant relationships from a generalised linear model with Poisson errors of species richness ~ log[canopy extent] + host, and in (c) a model with binomial errors of the ratio of alien to native species richness ~ log[canopy extent] (see also Table 3).

proportion of aliens to natives in the subcanopy was greater closer to the base (Fig. 5; providing support for the role of propagule pressure in the invasion process (hypothesis 2)), greater on sandy sites and lower on calcrete sites, and also increased with canopy extent (Table 3d). Much of the explanatory power of these factors was spatially auto-correlated, with only canopy extent significantly affecting the proportion of aliens to natives in the trend surface model.

The same minimum adequate models and qualitative results were obtained for all three species richness measures and for the proportion of native species to alien species when only subcanopy fleshy-fruited individuals greater than 0.1 m in height were considered.

ASSEMBLAGE COMPOSITION

A total of 158 trees were used in the comparison of subcanopy assemblages beneath *A. tortilis* and *Prosopis*, after seedlings were removed and trees with no other fleshy-fruited subcanopy plants excluded. Subcanopy assemblages were significantly different beneath *A. tortilis* and *Prosopis* canopies (Global statistic $R = 0.143$, $P < 0.01$).

An analysis of the species contributing most to the observed differences revealed that the differences were primarily due to changes in relative abundance of native fleshy-fruited species (Table 4). Most species were more common under *A. tortilis*, although *Rhus lancea* was more common beneath *Prosopis*, and *Lycium cinereum* had comparable abundances beneath the two. Relative abundance of subcanopy fruited species differed between the two species. Beneath *A. tortilis* (in order of declining abundance), *P. campestris*, *Diospyros lycioides*, *R. lancea*, *Ziziphus mucronata* and *L. cinereum* were the most common species. Beneath *Prosopis* the order was *R. lancea*, *P. campestris*, *D. lycioides* and *L. cinereum.*

Comparison of only the alien component of fleshy-fruited species found no significant differences between host tree species or distance from military base, although their assemblage composition differed with canopy extent ($P < 0.01$). Here, *Celtis* sp. and *Schinus molle* were far more common beneath large trees, and *Echinopsis spachiana* was more common beneath small trees. Again, this provided no evidence in support of alien host plants facilitating invasions more than native host plants (hypothesis 3).

Discussion

Birds facilitate the movement of alien plant species from gardens into a variety of natural and anthropogenic ecosystems (Glyphis *et al.* 1981; Ferguson & Drake 1999; Dean & Milton 2000; Gimeno & Vila 2002; Gosper *et al.* 2005; Buckley *et al.* 2006). In so doing they assist plants to overcome an important barrier to invasion, namely seed dispersal (Richardson *et al.* 2000b). By dispersing plants in a directed way to potentially suitable microsites, birds may also help invaders over various additional obstacles to invasion. Thereafter, the components of invasion risk (probability and impact) are more difficult to predict because they vary with species, ecosystems, interactions and feedbacks.

Our study tested three hypotheses, namely: that invasion is aided by host trees (for which we found strong support); that propagule pressure determines invasion probability (again strongly supported); and that alien host plants are better facilitators of alien fleshy-fruited species invasions than are native hosts (not supported).

IMPORTANCE OF HOST TREES AS ESTABLISHMENT SITES

Although the evolution of fruit for directed dispersal may only be a secondary adaptation (Mack 2000), directed dispersal to suitable sites can reduce seedling mortality and consequently raise fitness (Howe & Smallwood 1982; Wenny 2001), suggesting that evolution of fruit confers the advantage of arrival in suitable establishment sites (Howe & Smallwood 1982). Dispersal to sites in the savanna was mainly by birds or bats, and most fleshy-fruited plant species established only in microsites beneath tree canopies. Performance of fleshy-fruited seedlings may be better in subcanopy sites than in the open (Milton *et al.* 1997), although this does not apply to all fleshy-fruited plants when they reach maturity (Seymour 2006), nor are shaded sites a

Table 4 Subcanopy species contributions to differences in assemblages beneath *A. tortilis* and *Prosopis* host trees. Numbers in bold indicate higher abundance compared between the two host-tree species

Fleshy-fruited species	Average abundance beneath *A. tortilis*	Average abundance beneath *Prosopis*	Average dissimilarity	Dissimilarity/ standard deviation	Percentage contribution	Cumulative percentage
Pollichia campestris	**4.14**	2.56	16.10	0.82	20.92	20.92
Diospyros lycioides	**4.45**	2.31	13.31	1.04	17.30	38.22
Rhus lancea	2.87	**3.50**	12.03	1.02	15.63	53.85
Lycium cinereum	1.88	**2.00**	9.10	0.81	11.82	65.67
Ziziphus mucronata	**2.73**	1.56	8.24	1.02	10.71	76.38
Celtis sp.	**1.33**	1.06	4.86	0.62	6.32	82.70
Lycium hirsutum	**0.92**	0.47	3.17	0.61	4.11	86.81
Asparagus cooperi	**0.88**	0.19	2.58	0.56	3.35	90.16

prerequisite for successful establishment of all fleshy-fruited plants (Dean & Milton 2000). Nucleation then arises because seeds of fleshy-fruited alien plants are directed to subcanopy sites by frugivores such as birds or bats. Dispersal of seeds by frugivorous birds is generally clumped beneath perch sites (Snow 1976; Milton *et al*. 1997; Holl 1998). We assume that the observed association of alien fleshy fruited plant species with tree canopies was primarily the result of dispersal by birds, because vervet monkeys (*Cercopithecus aethiops*), while occurring sporadically in this area, are not sufficiently common to have a significant impact on seed rain to canopy sites (W. R. J. Dean, personal observations).

Seeds of alien plants dispersed to the savanna ranged in diameter from 1 mm (*Ficus carica*) to 8 mm (*Melia azedarach*), within the range taken by the most common frugivorous birds in this system, namely Red-faced Mousebirds (*Urocolius indicus*), Acacia Pied Barbets (*Tricholaema leucomelas*), African Red-eyed Bulbul (*Pycnonotus nigricans*) and Cape Glossy Starlings (*Lamprotornis nitens*) (Seymour 2006). Some alien fruits also resembled those of native plants in size, colour and texture. For example, the fruits of *Celtis* sp. (yellow and leathery) resemble those of the native species *Ziziphus mucronata* and *Grewia flava*, while those of *Schinus molle* and *Rhus pendulina* are very similar to those of local *Rhus* species. As monkeys are uncommon, and as there are no indigenous plant species with large dispersal units resembling those of *Citrus* sp. or *Maclura pomifera*, it is unlikely that indigenous birds would be able to open up these fruits and disperse the seeds.

We have shown that, in the absence of host trees which attract birds and provide subcanopy sites where conditions are favourable for seedling establishment, alien fleshy-fruited plant species would either fail to be dispersed from gardens into savanna, or would fail to establish there. Host trees are therefore essential for invasion of savanna by fleshy-fruited plants.

PROPAGULE PRESSURE AND INVASION PROBABILITY

Propagule pressure is a crucial mediator in the interplay of the numerous factors that determine the success of an invasive species (review in Richardson & Pyšek 2006).

For species that potentially had a high propagule pressure but are not invading, there were easily identifiable barriers to dispersal and establishment, namely: low or non-viable seed production; absence of suitable dispersers, in particular for *Maclura pomifera*, *Poncrius* sp. and *Citrus* sp.; absence of suitable subcanopy establishment sites; or a lack of conditions required to break dormancy, e.g. *Rosa damascena* and *Pyracantha* sp. may have failed to invade because conditions were never cold and moist enough to promote germination (Anonymous 2005). However, the reasons for some of the other species, e.g. *Ligustrum lucidum*, not establishing outside the military base are unclear.

The presence and relative abundance of the various alien plant species cultivated in the military base probably reflects their net performance over the past 40 years. Although most of the gardens were irrigated, species suited to the ambient environmental conditions were probably planted more frequently or survived better. Consequently, the most common species on the base may be those best adapted to conditions in the surrounding vegetation. Smaller-seeded plants are also expected to be more efficiently dispersed (Levey 1987), but this effect was not seen here, perhaps because a limited suite of species can establish in this semi-arid environment.

Despite these exceptions, our study provides clear evidence that an abundant seed source (in the presence of suitable seed dispersers and host trees) will increase the probability of invasion of a natural ecosystem by alien species.

RECRUITMENT FREQUENCY

Our results show the net performance of the various alien species over several decades of fluctuating weather conditions. Size-class distribution for alien trees indicated that whereas some (*Celtis* sp., *Rhus pendulina*, *Schinus molle*) could already be objectively classified as invasive (Richardson *et al*. 2000b) on the basis of widespread distribution of seedlings and ability to establish and reproduce in undisturbed savanna, others (*Brachychiton populneus*, *Ficus carica*) were well dispersed but have yet to reach reproductive maturity. If the fire regime at the site was to change or there were several wet years, these species may recruit, but at present they have a low probability of invading this habitat type.

The relationship between seedling abundance and site occupancy for small seedlings of alien plants indicated that invasion of the savanna site sampled was still in a relatively early stage (Fig. 3). Large numbers of small seedlings occurred at a few sites but alien seedlings were not as well dispersed as those of natives. This was probably because they originated from the military base alone, or a few point sources for those species where individuals had reached reproductive maturity in the savanna.

Lawes *et al*. (2006) found that alien plants that were abundant locally tended to become abundant at landscape level and could be considered high-risk invaders. On the basis of this framework, *Celtis* sp., *Rhus pendulina* and *Schinus molle* pose the biggest invasion risks in the area and all three species require coordinated management action.

EXTRA-LIMITAL INDIGENOUS INVADERS

Two of the top five savanna invaders identified in this study, *R. pendulina* and *O. europaea* ssp. *africana*, are indigenous to South Africa and naturally occur within

200 km of the study site, *R. pendulina* in riparian woodland along the Orange River, and *O. europaea* ssp. *africana* on dolomitic soils on the Ghaap Plateau (Low & Rebelo 1996). As hypothesized, it would appear that the propagule pressure from plantings in the military base also enabled these species to invade Acacia savanna despite the habitat differences. Moreover, the most invasive species, *Celtis* sp., is probably a hybrid between the indigenous *Celtis africana* that occurs in forest pockets in higher altitude grassland to the east of Kimberley, and *C. australis* or *C. sinensis*, both of which are used as garden subjects. Hybrid seedlings have previously been reported from the suburbs around Pretoria in the Gauteng province of South Africa (Coates Palgrave 2002).

NATIVE VS. ALIEN HOSTS AND THE POTENTIAL FOR ECOSYSTEM TRANSFORMATION

Our hypothesis that alien host plants are better facilitators of alien fleshy-fruited species invasions than are native hosts was rejected. Both abundance and species richness of fleshy-fruited species were lower beneath alien *Prosopis* spp. than beneath indigenous *Acacia tortilis*, suggesting that, at this site, 'invasional meltdown' (*sensu* Simberloff & Von Holle 1999) is not implicated and that alien fleshy-fruited plants can infiltrate natural savanna woodland more easily than woodlands invaded by mesquite. In addition, as both native and alien fleshy-fruited species were more common beneath native host trees, replacement of native by alien hosts would see a decline in overall species richness. Dean *et al*. (2002) also found that fleshy-fruited species occurred at lower densities beneath *Prosopis* than *Acacia* species. This cannot be explained by different longevities of *Prosopis* sp. and *Acacia tortilis* because they have similar potential life spans of 100–200 years (Prince & van der Jeugd 1993; Flinn *et al*. 1994). Lower species richness below *Prosopis* might be because *Acacia* species offer better perches for frugivorous birds (Dean *et al*. 2002), or because *Acacia* species provide subcanopy environments more suitable for seedling germination and survival.

Although alien host trees do not promote invasion of alien fleshy-fruited plants more successfully than do native hosts, subcanopy plant assemblages differed significantly among host species. Alien hosts and subcanopy invaders may also respond differently to disturbances or alter a variety of species interactions, leading to unpredictable changes in vegetation dynamics. For example, alien plants that can invade relatively undisturbed ecosystems have the potential to transform them if they can out-compete indigenous plants for essential resources (Flores-Flores & Yeaton 2000), change successional dynamics of local savannas (Archer *et al*. 1988; Dean *et al*. 1999), or disrupt disperser or pollination mutualisms (Traveset & Richardson 2006). Whereas in natural savanna only *Rhus lancea* and occasionally *Ziziphus mucronata* are able to overtop their *Acacia* hosts, it is likely that the potentially taller alien species *Schinus molle* and *Celtis* sp. would do so more frequently, increasing mortality rates of native trees.

Phenologies of native fleshy fruiting species in the Kalahari are timed to minimize competition for dispersers and fruit. Fruit of *Rhus* spp. ripens in spring (September) followed by *D. lycioides* and *E. rigida* in summer (November–January), and later in autumn and winter (March–August) by *G. flava* and *Z. mucronata* (Coates Palgrave 2002), whereas *Asparagus*, *Lycium*, *Pollichia*, *Solanum* and *Thesium* spp. can fruit more than once annually following opportunistic flowering responses to large rainfall events (Milton *et al*. 2004). Alien species might out-compete native species for dispersers or change dispersal distances if they supply more fruit and overlap in fruiting phenology (Traveset & Richardson 2006). In addition, differences in subcanopy assemblage composition are likely to have implications for pollinators, invertebrate herbivores and dispersers.

Alien species also have the potential to change the intensity of fires beneath tree canopies. Fire often kills large trees, and changes in understorey species composition and leaf biomass are likely to change the way the fire burns (e.g. temperature, position and duration). Seymour (2006) found that fire decreased cover of fleshy-fruited plants in Kimberley savanna, but that some species could resprout. Differences between alien and native trees in longevity, flammability and resprouting ability may affect the potential of alien invaders to transform Kalahari savanna.

Conclusions

It is clear that the system will be changed by the infiltration of alien (including indigenous extra-limital) species. Invasive species can potentially change dispersal dynamics. Indigenous fleshy-fruited species in this area compete for dispersers, as there is almost always a surfeit of fruit on subcanopy plants, so alien species are likely to increase that competition. Of the native species recorded, only *R. lancea* overtops the shade-intolerant *A. tortilis*. However, at least two of the alien species, *S. molle* and *Celtis* sp., also have this potential, and so the invasion may increase the likelihood that a host tree is over-topped, shaded and killed. On a positive note, the management of invasive species can concentrate on the subcanopy environments, as these are the only sites where the fleshy-fruited alien species can establish.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Examples of size-class distributions for individuals of three alien fleshy-fruited species

Appendix S2 Examples of species distributions.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01247.x

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